

Computation in the Learning System of Cephalopods

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Abstract. The memory mechanisms of cephalopods consist of a series of matrices of intersecting axes, which find associations between the signals of input events and their consequences. The tactile memory is distributed among eight such matrices, and there is also some suboesophageal learning capacity. The visual memory lies in the optic lobe and four matrices, with some re-exciting pathways. In both systems, damage to any part reduces proportionally the effectiveness of the whole memory. These matrices are somewhat like those in mammals, for instance those in the hippocampus.

The first matrix in both visual and tactile systems receives signals of vision and taste, and its output serves to increase the tendency to attack or to take with the arms. The second matrix provides for the correlation of groups of signals on its neurons, which pass signals to the third matrix. Here large cells find clusters in the sets of signals. Their output re-excites those of the first lobe, *unless* pain occurs. In that case, this set of cells provides a record that ensures retreat.

There is experimental evidence that these distributed memory systems allow for the identification of categories of visual and tactile inputs, for generalization, and for decision on appropriate behavior in the light of experience.

The evidence suggests that learning in cephalopods is not localized to certain layers or “grandmother cells” but is distributed with high redundancy in serial networks, with recurrent circuits.

Introduction

Responding appropriately in a complex environment depends upon the categorization of events and a decision of what to do. Animals with good brains have the ability to learn the useful responses to particular events that they encounter. They may not be born with receptors tuned

to identify objects or situations, say a rock or a tree or a fish, but learn the classification of particular sets of stimuli by virtue of the large number of their neurons. It has been claimed that this involves simply “the spontaneous emergence of new computational capabilities from the collective behaviour of large numbers of simple processing elements” (Hopfield, 1982). Biologists will probably suspect that a genetic component is involved in the organization.

Cephalopods have such nervous systems with numerous neurons, and there is sufficient information about their arrangement to suggest how they function. Formerly, I have emphasized that the circuits in their brains must allow for the outputs from feature detectors to produce alternative effects after learning (Fig. 1). I proposed that the feature detectors must become restricted during learning to establish units of memory or mnemons. This view is correct in that it emphasizes the possibility of alternative outputs from feature detectors, but it is much too restrictive. Emphasis on units obscures the essential fact that these are systems with numerous parallel, interacting channels. It is now evident that the various lobes of the brain provide sequences of matrices of intersecting axes, with feedback. They enable the identification of categories of input and storage of records of the probable value of each, in the form of bias to particular directions of action to each set of input signals.

The principle of the matrices is to provide for selection of paths that are used and inhibition of those that are not used. This is accomplished by various means that allow interaction between pathways. One of the best analyzed systems is in the mammalian hippocampus (Fig. 2) (Rolls, 1990). In a competitive learning matrix such as the dentate gyrus, “different input patterns on the horizontal axons will tend to activate different output neurons. The tendency for each pattern to select different neurons can be enhanced by providing inhibition between the output neurons. . . . Synaptic modification then occurs. . . and

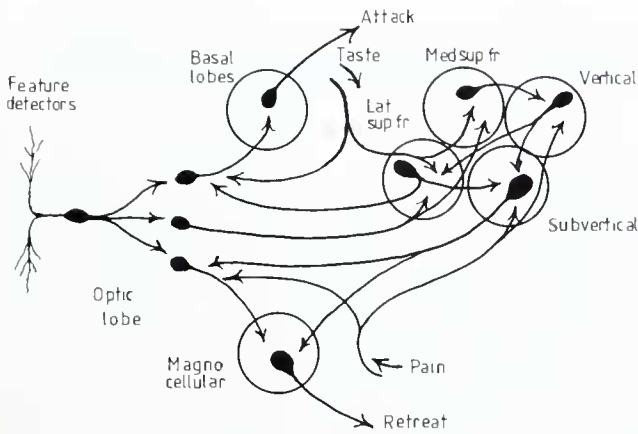


Figure 1. Scheme to show alternative pathways from the visual feature detectors of an octopus. There are output pathways for attack or retreat. A third pathway leads to the four matrices of the vertical lobe system. Here particular patterns of visual signals are combined with those of taste to increase the future tendency to attack, or with signals of pain to reduce it.

the response of the system as a categorizer climbs over repeated iterations” (Rolls, 1990).

In autocorrelation networks, such as the CA₃ cells (Fig. 2), the preferred pathways are reinforced by mutually strengthening each other. In this case, the cells of the matrix have collaterals that feed back to their own inputs. These recurrent synapses follow the Hebb rule so that “any strongly activated cell or set of cells

becomes linked by strengthened synapses with any other conjunctively activated cell or set of cells” (Rolls, 1990). As a result, during recall “presentation of even part of the original pattern . . . comes to elicit the firing of the whole set of cells that were originally conjunctively activated.”

In the hippocampus, this result is achieved by the collaterals of the CA₃ cells, which reactivate the dendrites of their own and a large number of other CA₃ cells. It may be that in cephalopods a similar effect is achieved by passing the signals through a series of lobes, each serving as a matrix whose output may be returned to a previous member of the series (Fig. 3). The functioning of any such matrix system depends on the particular anatomical arrangements and details of synaptic functioning and its alteration with use. We do not know enough about such factors in cephalopods to be able to specify precisely how they operate. However, the system is simple enough to allow us to follow the whole sequence through these lobes, from sense organs to motor output, and at least to speculate about its functioning.

Matrix systems of this sort have the properties that we associate with complex animal behavior. They ensure that there is *generalization*: presentation of even a part of the original figure, or one like it, activates the firing of the whole set of cells that were conjunctively activated (“*completion*”). Moreover, the system continues to operate even if some of the cells fail to operate or are removed (“*fault tolerance*”). We can show that these essential

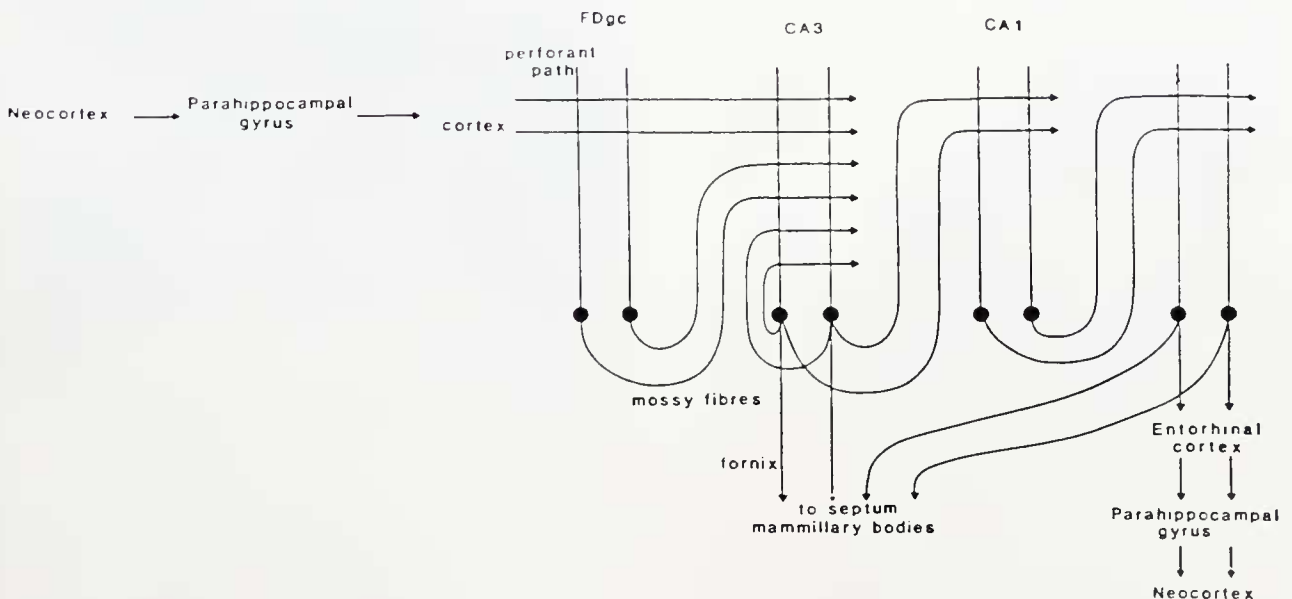


Figure 2. Schematic representation of the scheme of matrices and connections within the primate hippocampus and with the neocortex. The competitive matrix in the dentate gyrus leads to an auto association matrix formed by the CA₃ cells, which in turn lead to a competitive matrix on the CA₁ cells (From Rolls, 1990, with permission).

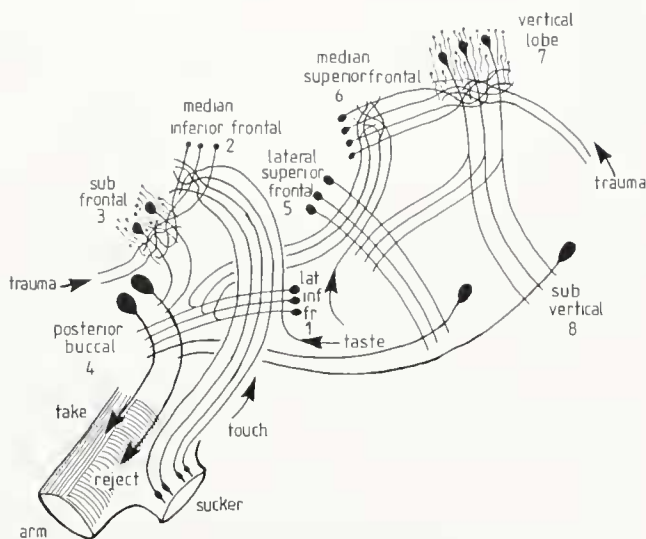


Figure 3. Diagram of the connections of the tactile memory system of *Octopus*. The successive matrices are labelled 1 to 8. In addition, there is some learning capacity in the suboesophageal centers.

properties of memory systems are present in the nervous system of octopuses.

The nervous system of an octopus provides for categorization and setting up of memories both for vision and touch. There are two distinct systems, each made up of four lobes, with elements whose arrangement can now be seen to constitute sequences of matrices (Fig. 3, 4). It was thought at one time that these were independent visual and tactile systems, but it is now clear that in tactile learning all eight lobes are involved (Young, 1983). This, therefore, constitutes a remarkable example of a distributed memory system using a series of networks. This model is rather similar to that suggested by Wells (1978). It does not depend on detailed preformed connections and so avoids problems of complex morphogenesis.

The Chemo-Tactile Memory System

Octopuses readily recognize differences in the chemical nature and texture of objects by touch, although they cannot discriminate between shapes (Wells, 1978). The receptors for touch are in the rims of the suckers (see Graziadei in Young, 1971). Their axons proceed through synapses in the arm, but no details are known of the coding signals that are sent to the brain.

In our experiments, Wells and I train octopuses to distinguish between plastic balls, either smooth or with up to thirteen incised rings (Wells, 1978; Young, 1983). We train an animal by giving it food when it takes one ball (say a smooth one) and by giving it no reward or a small electric shock for taking the other (rough) (Fig. 5). In critical experiments, the optic nerves are cut to avoid possible

visual discrimination. Many of the experiments are done after the whole supraoesophageal lobe has been bisected. The arms of the two sides then learn independently and can even be trained in opposite directions.

Afferent fibers from the arms and also taste fibers from the lips cross the dendrite systems of the first tactile lobe, the lateral inferior frontal (Fig. 6, 7). The axons of the cells of this first lobe pass partly to the fourth lobe, the posterior buccal, and partly to the lateral superior frontal and so to the vertical lobe system (below). The fibers from the arms and lips then pass on to the second matrix, in the median inferior frontal, where they interweave and cross the trunks of a large sample of the 10^6 cells, this allows maximum opportunity for any cell of the lobe to receive signals from a variety of input fibers (Fig. 7). These median inferior frontal cells then send their axons to the third matrix, the subfrontal lobe, which contains relatively few large cells with twisted trunks and many bushy dendrites and, in addition, a great number (5×10^6) of very small amacrine cells. The subfrontal also receives numerous fibers from below, presumed to signal trauma. The large subfrontal cells send their axons to the fourth lobe, the posterior buccal, from which, in turn, large axons pass directly to the arms and cause them either to draw in or reject the object touched (Budelmann and Young, 1985). These cells must be of two sets, some causing the object touched to be drawn in, the others to reject it.

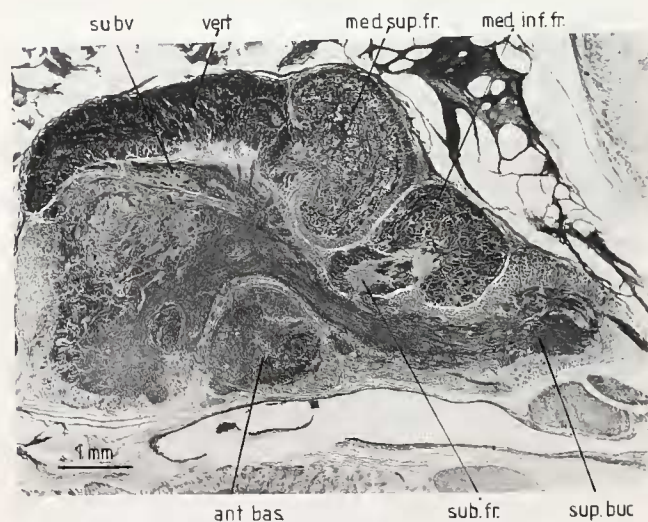


Figure 4. Sagittal section of the supraoesophageal lobe of *Octopus vulgaris* stained with Cajal's silver method. Abbreviations for all figures: ant. bas., anterior basal; b. med., median basal; buc. p., posterior buccal; cer. br. con., cerebrobrachial connective; cer. tr., cerebral tract; lat. inf. fr., lateral inferior frontal; lat. sup. fr., lateral superior frontal; mag., magnocellular; med. inf. fr., median inferior frontal; med. sup. fr., median superior frontal; op., optic; ped., peduncle; post. buc., posterior buccal; plex., plexiform layer; prec., precommissural; pv., palliovisceral; ret., retina; subfr., subfrontal; sup. buc., superior buccal; subv., subvertical; vert., vertical.

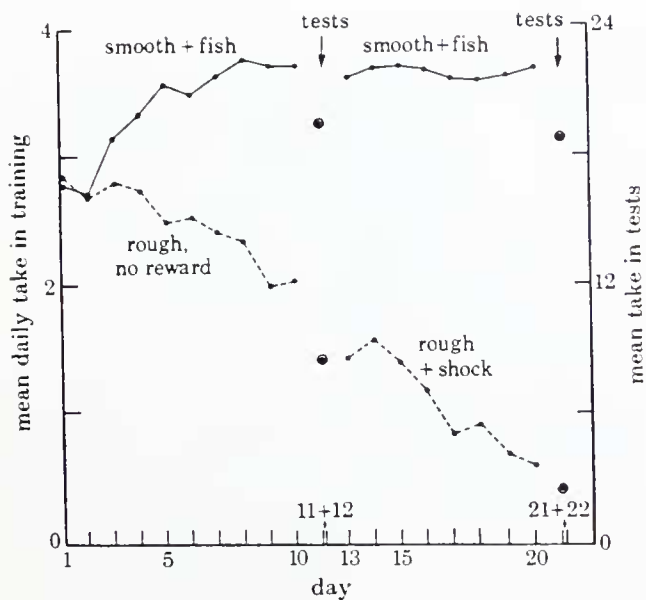


Figure 5. Sequence of learning by 129 control half brains to take a smooth ball and reject a rough. Four trials daily. On days 11 and 12, and 21 and 22, the figure shows mean takes out of 24 unrewarded tests with each ball (Young, 1983).

The basic action of the system is that an arm cautiously and slowly draws in an unfamiliar object that it touches. If this proves to provide food, the taste signals from the lips activate cells of the lateral inferior frontal, which increase the tendency to take and perhaps operate as a competitive learning matrix (like the dentate gyrus). The pattern of input and taste signals is then passed on to the median inferior frontal where that proportion of cells that receive this pattern of signals of touch and taste is activated. This can be considered a re-coding of the input pattern on to a more sparse set of cells.

The axons of these cells then proceed through the interweaving bundles to the subfrontal, where they make connection with a still smaller set of large cells with complex dendritic fields, having also an input of fibers indicating pain. If trauma occurs and these pain fibers are also activated, then the large cells of the subfrontal operate the rejection neurons of the posterior buccal lobe. The synapses activated by this particular pattern of input become consolidated, presumably by the action of the large number of amacrine cells whose short axons end among the dendrites of the larger cells of the subfrontal lobe (Fig. 6).

The basic operation of the system is thus to take objects touched *unless* signals of pain arrive. Signals of taste set up a greater tendency to take by competitive learning in the lateral inferior frontal lobe. Signals of pain set up a tendency to reject that pattern of touch by modification of synapses in the subfrontal lobe. As good evidence of this it was found that, after lesions destroyed all the small

amacrine cells, an octopus failed to learn not to take objects from which shocks were received (see this paper and Wells, 1978).

The Vertical Lobe System and Touch Learning

The inferior frontal system contains the major tactile memory, but the vertical lobe also contributes. Experiments show that removal of the vertical lobe impairs the tactile memory, but removal of the median inferior frontal has no effect on visual learning.

The tactile signals enter the vertical lobe circuit through fibers from the lateral inferior frontal that enter the outer plexus of the lateral *superior* frontal lobe (Fig. 3). The vertical lobe system contains four lobes precisely similar to those we have described in the inferior frontal. The lateral superior frontal sends fibers to the subvertical lobe and from there fibers pass down the cerebral tract to the posterior buccal lobe (Fig. 6). This circuit through the lateral superior frontal is thus in a position to increase still further the tendency to take objects that have been associated with taste reward.

The signals for touch are then passed on from the lateral to the median superior frontal. Here the bundles are again interwoven, exactly as in the median *inferior* frontal. The 1.8×10^6 cells thus receive varied combinations of signals of touch and taste, and these are passed on again through

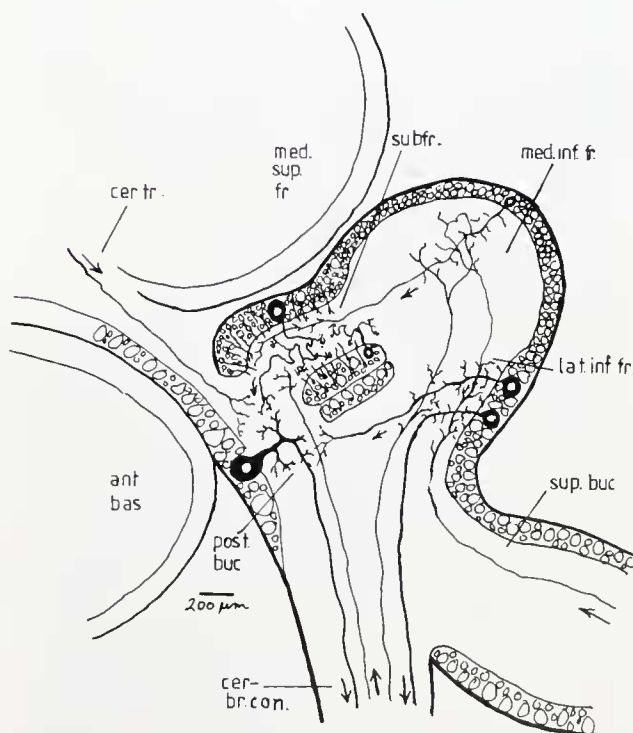


Figure 6. Diagram of connections in the inferior frontal system of an octopus (Young, 1971).

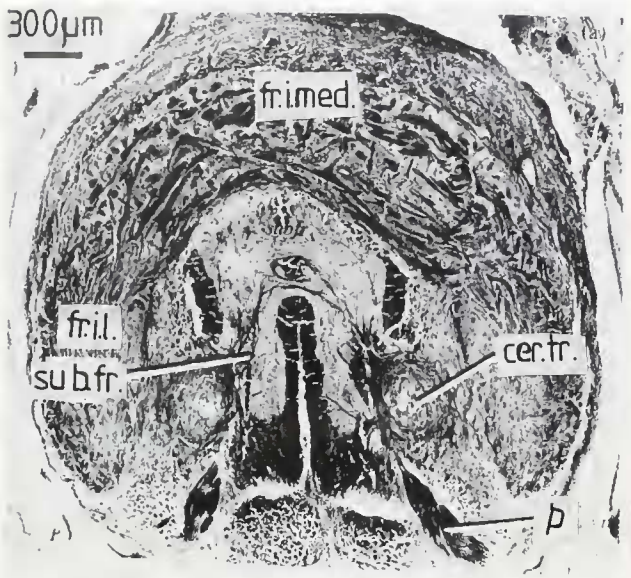


Figure 7. Transverse section of the inferior frontal system of *Octopus vulgaris* stained with Cajal's silver method. Abbreviations as Figure 4. cr. tr., cerebral tract (from subvertical lobe); p, tract of probably pain fibers from hind end of body.

a complex plexus to the vertical lobe. Here there are relatively few large cells (65,000), with complex dendrites, exactly like those of the subfrontal, and no less than 25 million amacrine cells.

The large cells send their axons down to the subvertical lobe and so to the posterior buccal, but also back to the lateral superior frontal (Fig. 3). This circuit evidently plays some part in re-enforcing the conjunctions, possibly by maintaining particular patterns by re-excitation.

The Distributed Tactile Learning System

The system for touch learning thus includes no less than eight distinct lobes with matrix structure (Fig. 3). The relative parts played by the various lobes was studied over a number of years in a large number of animals with divided brains. Lesions were made on one side, and the other was left as a control. In many of the experiments, discrimination was between completely smooth balls (0 rings) and those with 13 incisions. The sequence of training for 129 normal sides is shown in Figure 5.

A useful measure of the extent and reliability of discrimination is to give a series of 24 extinction tests with balls of differing roughness, shown at short intervals (1–3 min) without any reward. Such tests are arduous to give, but they show that habituation proceeds more slowly in proportion to similarity of each ball to the one for which reward was previously given (Fig. 8). The capacity for discrimination was also tested by using more nearly similar balls, with 4 and 7 rings. With long training, oc-

topuses could probably make some discrimination even between a difference of one ring.

By such tests we can compare the discrimination by animals after various lesions. Without the median inferior frontal there is still discrimination, but it is much less accurate than in control animals (Fig. 9). Removal of the vertical lobe also reduces accuracy, although to a lesser extent. Clearly each of the lobes through which the information passes adds something to the effectiveness of the representations that are formed, as would be expected from a system of matrices.

Animals without vertical lobes show errors largely when they take the negative ball, showing again that this lobe serves to increase the effectiveness of shocks. In normal octopuses, learning is possible even if rewards are delayed for up to 30 s after the ball has been removed. In animals without vertical lobes, such delay is no longer possible (Wells and Young, 1968). The re-excitation within the vertical lobe system serves to maintain the necessary excitability for a Hebb type of learning.

We have used this technique to make a large number of experiments, leaving one side as a control. With this technique it is possible to remove the subfrontal lobe, which cannot be approached laterally. The effect is to produce a complete inability to learn on that side: there is a strong and irreversible preference for the rougher balls (Young, 1983). The lobe evidently has some specific effect on the coding and discrimination process.

After cutting the cerebro-brachial tract (Fig. 6), the whole influence of the inferior frontal and vertical systems is removed. Nevertheless, there is still a slight capacity for learned discrimination (Fig. 10), which must lie in the suboesophageal ganglia, or in the arms themselves. This residual learning is difficult to study. Animals with these

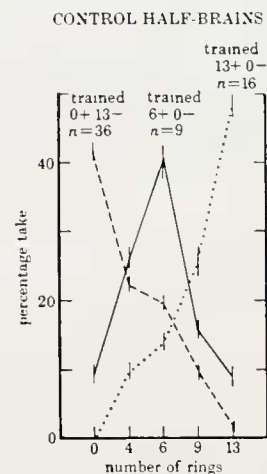


Figure 8. Tests after training in three different directions. Means and standard errors of ratios of takes of each ball to total takes, with 24 trials with each ball. The bars show standard errors.

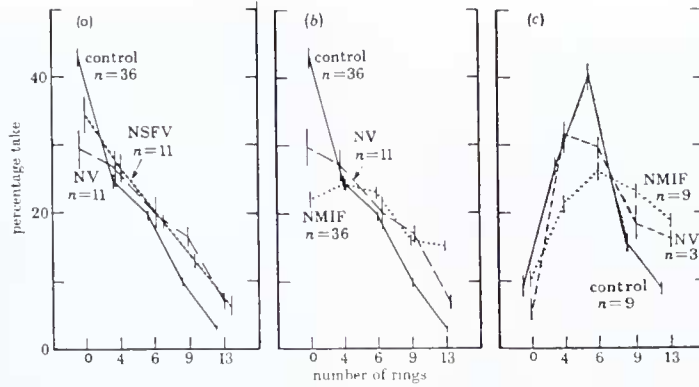


Figure 9. Tests after training. Comparison of results: 11 animals after cutting the tract between superior frontal and vertical lobes on one side (NSFV) and removing the vertical lobe (NV) on the other side; 36 controls for comparison (b): 36 animals after removing the median inferior frontal (NMIF); controls and NV added for comparison. In a & b, all training was with smooth balls positive and 13 rings negative. In (c) balls with six rings were positive and smooth balls negative. The figure shows the results for nine animals with the median inferior frontal removed on one side three animals with no vertical lobe on one side added for comparison. Note that here (and Fig. 8) the balls with 9 and 13 rings were seldom taken, although they had not been associated with shock.

large operations do not feed well and tend to hold pieces of food and other objects close to the mouth. Nevertheless, the differences in numbers of takes of the balls during tests are significant and show that some learning has occurred.

Some measure of the accuracy of the memory after the various lesions is given by the difference between the takes of the rough and smooth balls in the tests (Table 1). Using the difference in controls as a standard (100%), we can judge that animals without vertical lobes are rather less than half as efficient, without the median inferior frontal are one third as efficient, and that the suboesophageal contribution is about one sixth. Damage to the subfrontal produces a perverse effect.

The Visual Memory System

The vertical lobe system, which plays a part in tactile learning, forms, with the optic lobes, the main and only

component of the visual learning system. The existence of this double capacity is a striking demonstration of the power of such a distributed matrix system to store a variety of inputs. It will be very interesting to investigate whether individual cells of the vertical lobe system play a part in both systems. In a study of combined visual and tactile training, no mutual interactions between the two modalities was seen (Allen *et al.*, 1986).

The study of visual memory is made difficult by the complexity of the connections in the optic lobes, which are not fully understood. Cells with large tangential dendrites in the plexiform layer probably act as feature detectors (Fig. 11). Their axons form columns proceeding to the center of the lobe, where they interact in an interweaving matrix of cells and fibers. Second or third order visual neurons then send axons to the central nervous

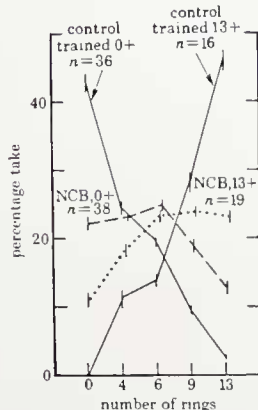


Figure 10. Tests after training. Comparison of control sides with those with the cerebrobrachial tracts cut (NCB).

Table 1

Mean takes in final tests after various lesions

Lobe removed	Smooth ball (positive)	Rough ball (negative)	Difference	Percent accuracy remaining
None (controls)	20.22	2.44	17.78	100
Vertical	17.68	10.55	7.13	40
Median inferior frontal	16.32	10.69	5.63	32
Cerebro-brachial tract	13.78	10.94	2.84	16
Subfrontal	7.89	8.42	-0.53	—

The last column indicates the capacity for learned discrimination that remains after the lesions, estimated as a percentage of the differences in the controls.

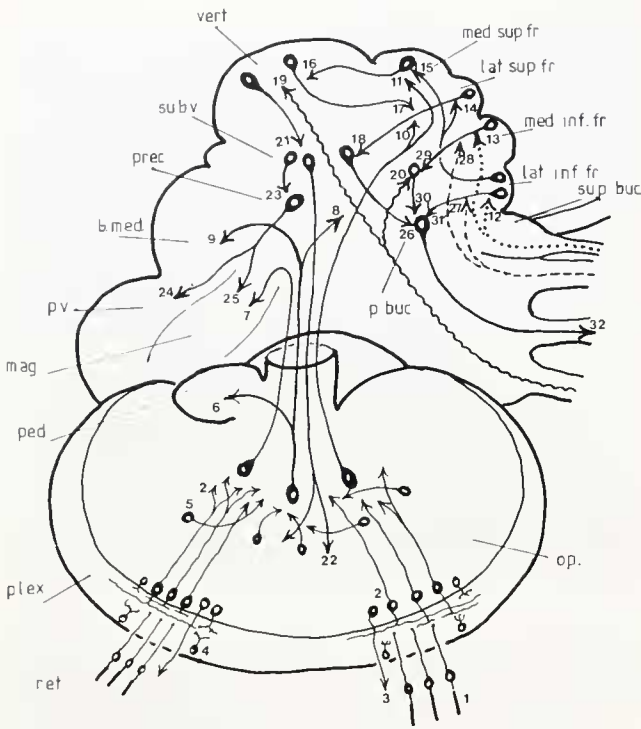


Figure 11. Diagram of the connections of the visual and tactile learning system of an octopus. 1, retina; 2, second order visual cells (feature detectors); 3, centrifugal cells; 4, amacrine cells; 5, tangential cells; 6, optic-peduncle; 7, optic-magnocellular; 8, optic-anterior basal; 9, optic-median basal; 10, optic-lateral superior frontal; 11, optic-median superior frontal; 12, taste fibers-lateral inferior frontal; 13, taste fibers median inferior frontal; 14, lateral inferior frontal-lateral superior frontal; 15, lateral inferior frontal-median superior frontal; 16, median superior frontal-vertical; 17, vertical-lateral superior frontal; 18, lateral superior frontal-subvertical; 19, pain fibers-vertical; 20, pain fibers-subfrontal; 21, vertical-subvertical; 22, subvertical-optic; 23, subvertical-precommissural; 24, precommissural-palliovisceral; 25, precommissural-magnocellular; 26, subvertical-posterior buccal; 27, chemo-tactile fibers-lateral inferior frontal; 28, chemo-tactile fibers-median inferior frontal; 29, median inferior frontal-subfrontal; 30, subfrontal-posterior buccal; 31, lateral inferior frontal-posterior buccal; 32, motor fibers from posterior buccal to arms.

system (Fig. 11). Some pass to the magnocellular lobe, and this is probably a pathway for rapid escape reactions. Other fibers pass to the peduncle and basal lobes, which together regulate movement, including attack. A third pathway leads to the superior frontal, and so to the vertical lobe, and is responsible for learned behavior.

The system is organized exactly as we have seen for tactile learning. In the lateral superior frontal, the visual fibers interact with those of taste, and this is a pathway that promotes attack. After removing this lobe from one side, an octopus will no longer attack when that eye has been used to see a crab, for instance, at a distance (Boycott and Young, 1955). The median superior frontal and vertical lobes provide a system that prevents visual attack when trauma occurs. After removal of these lobes or an

interruption of the circuit, an octopus will continue to make attacks, even at crabs, in spite of receiving shocks, *unless these shocks are given at intervals of five minutes or less*. "The setting-up of a memory representing association of a given situation with a shock is therefore a property of the optic and basal lobes but persistence of the representation depends upon the presence of the vertical lobe" (Boycott and Young, 1955).

Many other experiments have confirmed that learning of visual discrimination is impaired by lesions of the vertical lobe system (Young, 1961, 1965). If part of the vertical lobe is removed, the accuracy of the memory is proportionately reduced. This "graceful degradation" is a property to be expected in such a distributed system. Incidentally, Boycott and I were able to show that the same is true of the optic lobes. Memories are retained after removal of at least 50% of the lobe or after making lesions in several places with a cataract knife.

Discussion

The two memory systems of an octopus thus work on precisely similar principles. The input signals are passed through a series of matrices of intersecting axes allowing for particular groupings of signals to interact and to be directed to the pathways for attack or retreat. The systems are tuned to produce exploratory investigation of novel situations. If the results are favorable, the particular set of connections in the lateral frontal lobes are re-enforced by signals of taste, and this set later produces more rapid attacks or takes by the arms. The inputs are given further opportunity for interaction in the matrices of the median frontal lobes. In the vertical and subfrontal lobes, particular sets are then concentrated into rather few large cells. The recurrent output from these to the lateral superior frontal lobe presumably re-enforces the tendency to positive action, unless pain occurs. In that case, the other outputs from these large cells of the vertical or subfrontal prevent further investigation of that configuration of inputs. The numerous amacrine cells in these lobes are evidently concerned with establishing the conjunction between particular sets of input signals and the pathways of retreat.

The organization of these lobes, and the effects of removing them, suggests that learning in these animals is not localized to one or two "hidden layers" or to a few essential "grandmother cells," but is distributed with high redundancy in a series of matrices networks, with recurrent circuitry, up to a late stage where funneling to a few cells occurs.

We can gain some insight into how this process has evolved by considering the differences between octopods and decapods. Cuttlefishes and squids have a system of matrices for visual learning similar to that of octopods

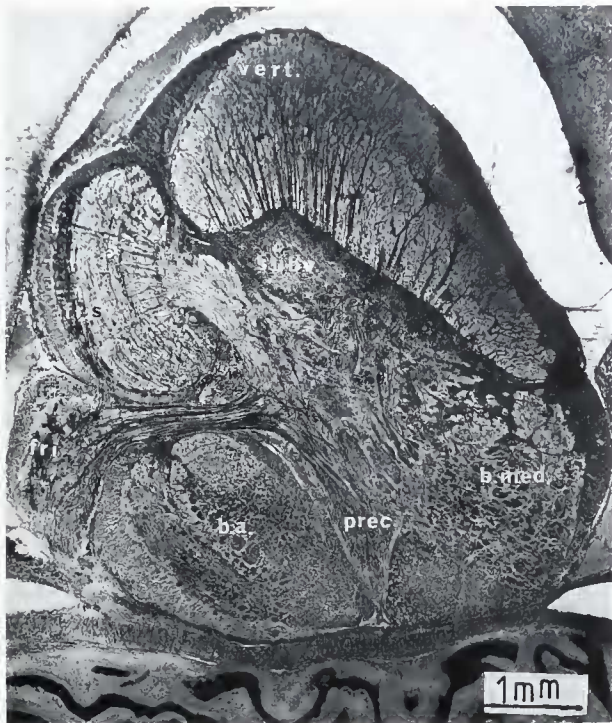


Figure 12. Sagittal section of the brain of *Sepia*. Note that there is no median inferior frontal or subfrontal. The superior frontal has a matrix structure like that of *Octopus*. The vertical lobe has a rather different structure. Cajal silver stain. b.a., anterior basal; b. med., median basal; fr. i., inferior frontal; fr. s., superior frontal; prec., precommissural; subv., subvertical; v., vertical.

(Fig. 12). In an early experiment it was shown that interruption of the vertical lobe circuit damages the visual memory system of *Sepia* (Young, 1938; Sanders and Young, 1940). This was the first suggestion that the circulation of impulses around a circuit provides a basis for memory (Fig. 13). There has been little further progress because the experiments are more difficult than in octopods. In decapods, the inferior frontal system is much simpler than in octopods: there is no median inferior frontal or subfrontal lobe. These animals detect the prey visually and often seize by ejection of the tentacles. It seems likely that they have, at best, only a small capacity for learned tactile discrimination; the operations of manipulating and eating the prey are complex, but are probably largely reflex. Nevertheless, there must be a mechanism for release of any object that gives pain when it is held. Probably all reflex systems have some method of inhibition, especially if they involve muscles acting reciprocally, such as flexors and extensors in mammals, where the inhibition is produced by Golgi type II cells in the spinal cord. In cephalopods, reciprocal inhibition is probably produced by the smaller amacrine neurons that are common among the larger motorneurons of the superior buccal and suboesophageal centers (Fig. 14). These mi-

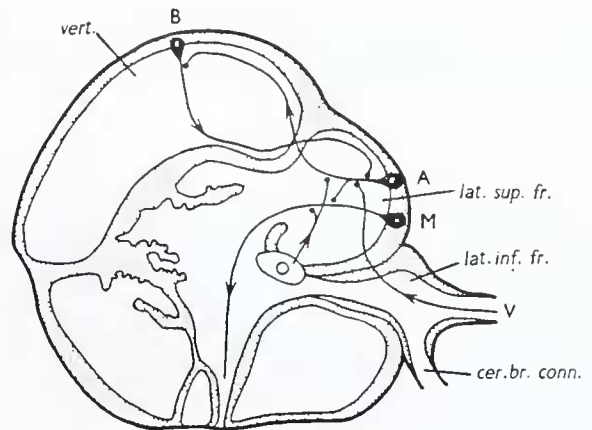


Figure 13. An early suggestion of re-excitation as the basis of memory. Diagram of *Sepia* to show how circulation between the lateral superior frontal (lat. sup. fr.) and vertical (vert.) might facilitate the firing of a motorneuron (M) by conjunctive excitation from the optic lobe (O) and taste fibers (V) (Young, 1938).

croneurons have processes restricted to a limited field, where they may serve to repress activity in the larger cells. In this context, it is especially interesting that we found some simple capacity for tactile memory in the suboesophageal lobes.

It is suggested that the amacrine cells of the subfrontal and vertical lobes of octopods have evolved from inhibitors of the reciprocal feeding reflexes. The inferior frontal and vertical lobe systems are backward extensions of the superior buccal lobes (see Fig. 4). The matrices that are responsible for learning have evolved by the modification of these simpler reflex centers. The incoming afferent fibers have become marshalled into rows crossing the axons of cells of the lobe, allowing the formation of conjunctive response to the incoming patterns of stimuli. The amacrine cells became collected together in distinct lobes, serving to prolong the effects, perhaps especially of inhib-



Figure 14. Drawing of a single large cell from the pedal lobe of *Loligo*, accompanied by very small cells with branches in the neighborhood.

itory inputs. The details are far from clear, but this provides a possible scenario for the evolution of memory mechanisms, at least among cephalopods.

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